

HABITAT CORRELATES AND DISTRIBUTION OF
CORDYLANTHUS MARITIMUS (SCROPHULARIACEAE)
ON TOMALES BAY, CALIFORNIA

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ABSTRACT

A study of 35 colonies of *Cordylanthus maritimus* subsp. *palustris* in salt marshes of Tomales Bay, California, revealed habitat relationships, including patterns of co-occurrence and cover values of associated species, and examined the possible effects of spatial distribution on the occasional failure of annual colonies to appear. The presence of hemiparasitic *C. m.* subsp. *palustris* was strongly associated with the presence of *Triglochin concinna* and *Limonium californicum*. Covariance of cover values within a large colony of *C. m.* subsp. *palustris* corroborated the survey results for *T. concinna*, but was inconclusive for *L. californicum*. Increased species richness and decreased vegetation height were also valuable predictors of greater *C. m.* subsp. *palustris* cover. A three-year investigation of biogeographic relationships suggested that annual probability of a colony to appear was influenced predominantly by patch size and *C. m.* subsp. *palustris* density rather than by sizes or distances of other nearby colonies or populations. We speculate that this reflects very low probabilities of seed dispersal among *C. m.* subsp. *palustris* colonies.

Cordylanthus maritimus Benth. subsp. *palustris* (Behr) Chuang and Heckard, Point Reyes bird's beak, is an annual salt marsh species that occurs along the Pacific coast from Marin County, California, northward to southern Oregon (Chuang and Heckard 1993). It is considered rare throughout its range, and is threatened by loss of coastal salt marsh habitat but is not state or federally listed as threatened or endangered (Skinner and Pavlik 1994). The southern California subspecies, *C. m.* subsp. *maritimus*, salt marsh bird's beak, is state and federally listed as endangered (U.S. Fish and Wildlife Service 1985; Skinner and Pavlik 1994).

Cordylanthus m. subsp. *maritimus* requires a sparse plant canopy that provides high light penetration for seedling survival (Dunn 1987; Fink and Zedler 1989), adjacent upland vegetation that provides suitable habitat for appropriate insect pollinators (Lincoln 1985), reduced tidal inundation (Fink and Zedler 1990), and possibly, low salinities (<8 ppt) for germination (Dunn 1987). These requirements generally limit the occurrence of *C. m.* subsp. *maritimus* to the upper terraces and edges of salt marshes where such conditions may occur (Dunn 1987; Zedler et al. 1992). *Cordylanthus m.* subsp. *palustris* appears to be limited to similar high marsh habitat on Tomales Bay.

TABLE 1. UNIVARIATE ASSOCIATIONS BETWEEN *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* AND OTHER PLANT SPECIES IN SALT MARSHES ON TOMALES BAY, CALIFORNIA. * P < 0.05, ** P < 0.01, *** P < 0.001. ^a Log-likelihood ratio test of association between presence/absence of *C. m. subsp. palustris* and presence/absence of other species.

Species/variable	<i>C. m. subsp. palustris</i> at Walker Creek Delta (product-moment correlation)		<i>C. m. subsp. palustris</i> on Tomales Bay (proportion of sites sampled)	
	Percent cover (n = 87)	Present (n = 35)	Absent (n = 22)	Likelihood ratio test ^a
<i>Atriplex triangularis</i>		0.06	0.50	7.69**
<i>Distichlis spicata</i>	-0.068	1.00	0.82	1.96
<i>Frankenia salina</i>	0.080	0.60	0.45	0.58
<i>Grindelia hirsutula</i>		0.23	0.14	0.97
<i>Jaumea carnosa</i>	-0.353***	0.77	0.73	0.07
<i>Limonium californicum</i>	0.177	0.71	0.32	4.38*
<i>Salicornia virginica</i>	-0.331**	0.97	0.82	1.97
<i>Spergularia rubra</i>		0.17	0.50	3.45
<i>Triglochin concinna</i>	0.523***	0.83	0.14	14.28***
<i>Triglochin maritima</i>		0.43	0.27	0.72
Species richness	0.591***			
Vegetation height	-0.405***			

Although *C. maritimus* is a facultatively parasitic species, its distribution may result from narrow habitat preferences rather than from host specificity (Chuang and Heckard 1971; Vanderwier and Newman 1984). Therefore, the identification of existing populations and viable sites for protection and restoration may depend on adequate knowledge of habitat suitability. Fink and Zedler (1990) found that suitable sites for reintroduction or recovery of *C. m. subsp. maritimus* populations were limited, but that site selection can benefit from an assessment of indicator species. The minimum size and most productive configuration of patches is also potentially important in recovery efforts because colonies of *C. m. subsp. maritimus* (Fink and Zedler 1990) and *C. m. subsp. palustris* (this study) can completely fail to appear in some years, although they may persist as seeds.

Plant species composition of upper salt marsh elevations where *C. m. subsp. palustris* occurs included several species (Table 1; nomenclature follows Hickman 1993) of varying abundance and distribution in northern California salt marshes (Macdonald 1988). Our first objective of study was to analyze patterns of co-occurrence of *C. maritimus* with other salt marsh plant species among populations on Tomales Bay, California. Secondly, to examine cover relation-

ships, we measured covariation of species cover values within the largest colony. Finally, we used data from the first three years of a monitoring program to assess patterns annual probability of *C. maritimus* colonies to appear among 35 colony sites on Tomales Bay, California.

STUDY AREA

Tomales Bay is a flooded, coastal fault-rift valley approximately 20 km long and 1–2 km wide, about 45 km north of San Francisco (Galloway 1977; Fig. 1). The largest salt marshes in Tomales Bay occur on the deltas of Lagunitas Creek at the southern end of the Bay and Walker Creek near the northern end of the Bay (Fig. 1). Numerous other smaller perennial and ephemeral streams enter the Bay along the east and west shores, each associated with a smaller, generally insular, delta salt marsh.

The *C. m.* subsp. *palustris* colony at Walker Creek Delta where we sampled plant species cover occupied approximately 2.5 of 40 ha. of salt marsh habitat and was undivided by tidal drainage channels. A low natural levee along the main creek channel north of the colony prevented the direct flow of freshwater from Walker Creek onto the salt marsh terrace, except during coincidental periods of extreme high tides and heavy runoff. Normal flushing of the marsh occurred through a separate tidal drainage on the south side of the colony.

METHODS

Co-occurrence. From 9 July to 20 August of 1991, 1992, and 1993, field surveys of *C. m.* subsp. *palustris* colonies were conducted on all potential habitat on Tomales Bay. For the purposes of this study, we defined a “colony” as a discrete patch of *C. m.* subsp. *palustris* separated by at least 10 m from the adjacent patch; we defined a population as a group of one or more colonies within a discrete salt marsh area, separated from other marshes by points of upland or more than 100 m of open water. The outer perimeters of all *C. m.* subsp. *palustris* colonies were marked annually and mapped, and the areal extent of each patch estimated as the product of the longest axis through the colony and its average perpendicular (colony width). Because sample units varied with the sizes of colonies and uncolonized salt marsh areas, species-area and other spatial scale effects prohibited direct comparisons of species richness or other community differences between colonized and uncolonized areas. However, to characterize habitat occupied by each colony, we visually ranked by relative cover the three most dominant species, visually estimated average density of *C. m.* subsp. *palustris* (low = 1–5 plants per m²; medium = 6–15; high = >15), and measured the shortest

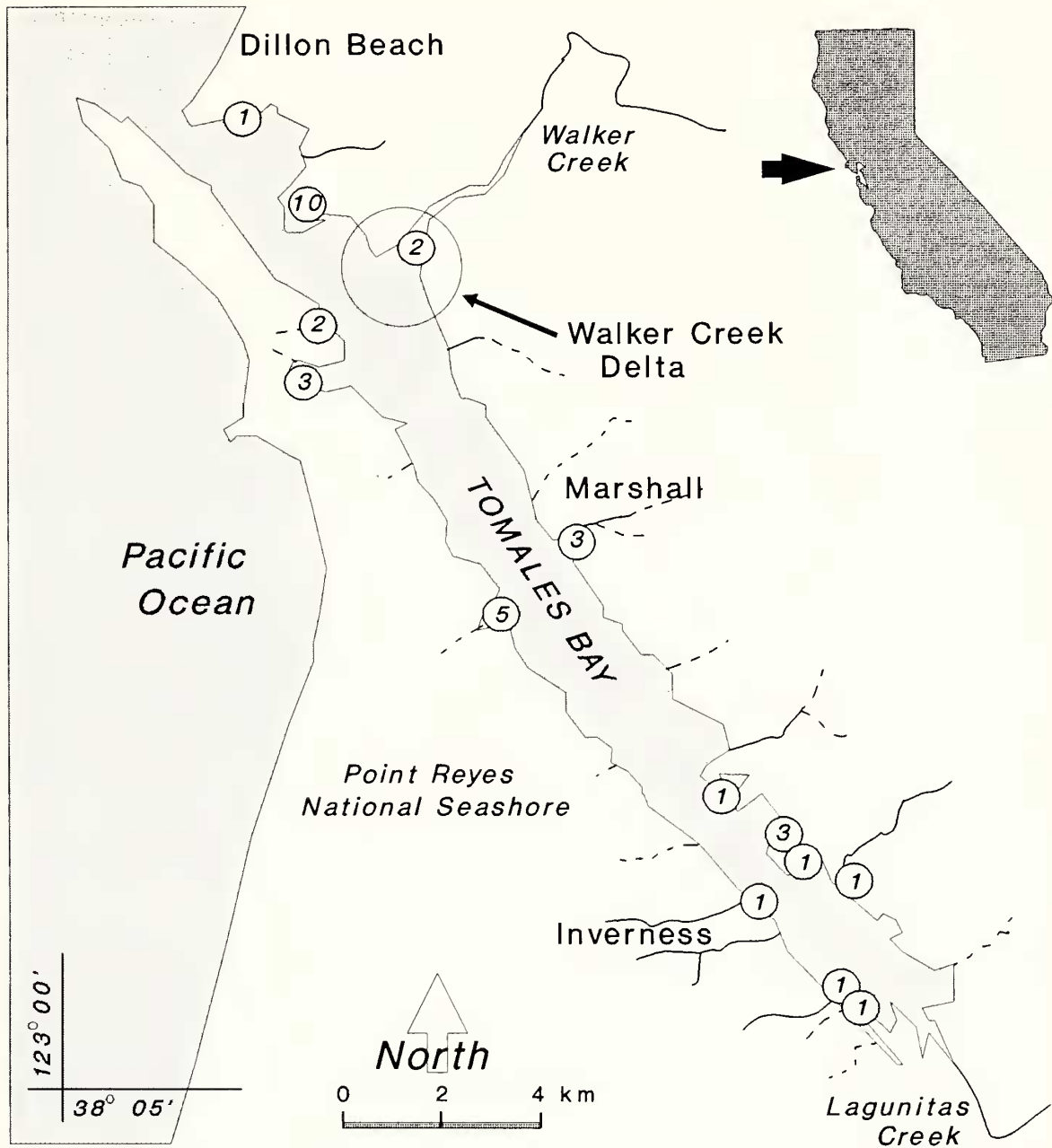


FIG. 1. Distribution of *Cordylanthus maritimus* subsp. *palustris* populations (defined by discrete salt marsh areas) on Tomales Bay, California. The circled number at each population site indicates the number of colony sites observed from 1991 to 1993.

distance to upland vegetation and freshwater drainage. At each colony, and at each salt marsh where *C. m.* subsp. *palustris* was not found, we listed all other plant species present.

To assess habitat suitability, we used stepwise logistic regression (SLR), a technique that does not assume multivariate normality among predictor variables. The classification performance of the SLR model was tested against a chance model, assuming a probability of correct classification of each group by chance proportional to group size (Titus et al. 1984).

Cover. At Walker Creek Delta on 22 August 1989, we plotted three parallel transects through the largest area occupied by *C. m.*

subsp. *palustris* on Tomales Bay (Fig. 1). The transects were 420 m long, 10 m apart, and aligned parallel to the overall elevational gradient of the salt marsh. Peak seed-set occurred approximately 4 weeks earlier. One-square-meter sample quadrats were placed at 15-m intervals along each transect, following a random start from the edge of the *C. m.* subsp. *palustris* patch.

Percent cover by species was measured using a wire grid with 10-cm grid intervals attached to a square-meter sampling frame. The observer slid a straight section of wire vertically down each of the grid intersection points and recorded each species touched by the wire. The proportion of hits in each quadrat estimated percent cover by species. Next, the observer held the sampling frame level above each plot, approximating the plane of average vegetation height, then measured the height of the grid wires above the ground. Using stepwise multiple regression (SMR), we examined the relationship between (log-transformed) *C. m.* subsp. *palustris* cover values (dependent variable) and cover values of other plant species (independent variables); species richness and vegetation height were included as additional candidate (independent) variables in the analysis.

Biogeographic relationships. We assessed the annual probability of *C. m.* subsp. *palustris* colonies to appear, based on three years of monitoring colony sites on Tomales Bay. Stepwise multiple regression was used to examine linear relationships between the number of years colonies were observed (maximum = 3) and eight (log-transformed) independent variables measuring biogeographic relationships: colony size (area), population size (sum of colony areas), distance to nearest colony, distance to nearest population, size of nearest colony, size of nearest population, colony density (estimated as described above), and number of colonies in the population.

RESULTS

We searched 35 salt marshes on Tomales Bay and identified 35 colonies among 14 populations of *C. m.* ssp. *palustris*. Half of the populations included only one colony and the most fragmented population included 10 colonies (Fig. 1). Colonies generally occurred at upper elevations of salt marshes, often in narrow bands near upper salt marsh edges. All *C. m.* subsp. *palustris* colonies on Tomales Bay ($n = 35$) were near ungrazed upland vegetation, usually mixed coastal prairie dominated by annual and perennial grasses (mean distance ± 1 SD = 18.0 ± 21.7 m, $n = 35$). Most colonies were also near sources of freshwater runoff (creeks or seeps; mean distance = 106.6 ± 170.3 m) and near plant species associated with freshwater or brackish habitat (mean distance = 36.4 ± 92.8 m).

The mean size of *C. m.* subsp. *palustris* colonies on Tomales Bay was 891 ± 4242 m²; however, most colonies were much smaller

TABLE 2. REGRESSION ANALYSES OF *CORDYLANTHUS MARITIMUS* SUBSP. HABITAT ON TOMALES BAY, CALIFORNIA. Tomales Bay-wide variation is analyzed with stepwise logistic regression (SLR) of presence/absence of *Cordylanthus maritimus* subsp. *palustris* (n = 57) on the presence/absence of co-occurring plant species in Tomales Bay salt marshes. Within-population variation is analyzed with stepwise multiple regression (SMR) of *C. m.* subsp. *palustris* cover (n = 87) on cover values of co-occurring plant species and species richness at Walker Creek Delta, Tomales Bay. * P < 0.05, ** P < 0.01, *** P < 0.001. ^a Probability cutpoint selected to balance correct classifications between groups.

Variable	<i>C. m.</i> subsp. <i>palustris</i> (presence on Tomales Bay [SLR])		<i>C. m.</i> subsp. <i>palustris</i> (cover at Walker Creek Delta [SMR])	
	Coefficient	SE	Coefficient	SE
(Constant)	-1.217		11.095	
<i>Triglochin concinna</i>	2.234	0.764**	0.059	0.016***
<i>Limonium californicum</i>	1.810	0.831*	-0.121	0.050*
<i>Atriplex triangularis</i>	-2.820	1.100*		
Species/m ²			1.263	0.244***
Log-likelihood = -22.03***			Model F = 22.92***	
Percent correctly classified = 86.0 ^a			Adjusted R ² = 0.43	
Cohen's kappa = 0.71***				

(median = 30 m², range = 0.1–25,200). The mean areal extent of populations was 1861 ± 6079 m² but most populations were much smaller (median 225 m², range 3–25,400). Average density estimates were less than 5 plants per m² in 58.8%, 65.2%, and 70.8% of colonies in 1991, 1992, and 1993, respectively. Weighting colony areas by mid-class density estimates, we obtained a rough estimate of median colony size of 225 plants (range = 3–75,000) and median population size of 1198 plants (range = 9–75,600). The three most dominant species (ranked by cover) among colonies most often included *Distichlis spicata* (97.1% of colonies), *Salicornia virginica* (60.0% of colonies) and *Triglochin concinna* (54.3% of colonies).

Univariate results from the Tomales Bay-wide survey suggested that the presence of *C. m.* subsp. *palustris* was significantly associated with the presence of *Triglochin concinna* and *Limonium californicum*, and the absence of *Atriplex triangularis* (Table 1). Pearson product-moment correlations of species cover values at Walker Creek Delta revealed that *C. m.* subsp. *palustris* cover was significantly greater in areas with greater *Triglochin concinna* cover, decreased cover of *Jaumea carnosa* and *Salicornia virginica*, greater species richness, and lower vegetation height (Table 1). Mean vegetation height at Walker Creek Delta was significantly lower in quadrats with *C. m.* subsp. *palustris* (\bar{x} = 12.5 ± 3.1 cm, n = 36), than in quadrats without *C. m.* subsp. *palustris* (\bar{x} = 16.5 ± 5.6 cm, n = 51; t = 3.88, P < 0.001, df = 85). Mean species richness at Walker

TABLE 3. OBSERVED AND PREDICTED (STEPWISE LOGISTIC REGRESSION) PROBABILITIES OF *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* OCCURRENCE ON TOMALES BAY, CALIFORNIA. Sample areas (n = 57) varied in presence (X) or absence (–) of *Triglochin concinna* (TRCO), *Limonium californicum* (LIMO), and *Atriplex triangularis* (ATRI).

TRCO	LIMO	ATRI	No. sample units	Observed proportion	Predicted by model \pm SE
–	–	X	6	0.000	0.017 \pm 0.021
–	X	X	4	0.000	0.103 \pm 0.095
X	–	X	0	–	–
–	–	–	10	0.200	0.222 \pm 0.112
X	X	X	3	0.667	0.496 \pm 0.239
X	–	–	9	0.778	0.735 \pm 0.128
–	X	–	5	0.800	0.653 \pm 0.174
X	X	–	20	0.900	0.942 \pm 0.041

Creek Delta was significantly greater in quadrats with *C. m.* subsp. *palustris* ($\bar{x} = 6.7 \pm 0.8$, n = 36) than in quadrats without *C. m.* subsp. *palustris* ($\bar{x} = 4.8 \pm 1.4$, n = 51; $t = 7.33$, $P < 0.001$, $df = 85$).

Stepwise logistic regression (SLR) predicted the presence of *C. m.* subsp. *palustris* among Tomales Bay salt marshes 71% better than chance alone (Table 2). *Cordylanthus maritimus* subsp. *palustris* was associated with the presence of *Triglochin concinna* and *Limonium californicum*, and with the absence of *Atriplex triangularis* (Table 2); the predicted probability of *C. m.* subsp. *palustris* occurring if all three of these conditions were met was 0.94 (Table 3).

The stepwise multiple regression (SMR) of plant species cover values at Walker Creek Delta associated greater *C. m.* subsp. *palustris* cover with greater *Triglochin concinna* cover, lower *Limonium californicum* cover, and greater species richness (Table 2). However, these three predictors accounted for only 43% of the variation in *C. m.* subsp. *palustris* cover among quadrats (Table 2); species richness alone accounted for 35% of the variation ($r = 0.59$, n = 87, $P < 0.001$).

Fifty-seven percent of *C. m.* subsp. *palustris* colonies on Tomales Bay appeared in all three years, 14% in two of three years, and 29% in one of three years. The preliminary SMR of number of years colonies appeared suggested that stability of colonies increased with colony size and density, and decreased with the number of colonies in the population (Table 4). The inverse relationship with number of colonies in a population reflected the stabilizing influence of larger colony size but not larger population size: colonies in smaller groups were generally larger ($r = -0.42$, $P < 0.01$, n = 35) but were not associated with larger populations ($r = -0.04$, $P = 0.88$, n = 14). Increased stability among larger colonies was also reflected in a significant inverse correlation between colony size and its coefficient

TABLE 4. STEPWISE MULTIPLE REGRESSION OF NUMBER OF YEARS (MAXIMUM = 3) COLONIES OF *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* (n = 35) WERE PRESENT ON COLONY SIZE, NUMBER OF COLONIES IN THE POPULATION, AND DENSITY OF *C. M.* SUBSP. *PALUSTRIS* AT TOMALES BAY, CALIFORNIA. ** P < 0.01, *** P < 0.001.

Variable	Coefficient	SE
(Constant)	2.081	
Colony size (area)	0.162	0.048**
Number of colonies in the population	-0.579	0.191**
Colony density	1.128	0.375**
Model F = 11.28***		
Adjusted R ² = 0.48		

of variation among years ($r = -0.59$, $n = 35$, $P < 0.0002$). The model predicted that an isolated colony with one to five individuals per m², occupying 281 m² of habitat, would have an average annual probability of appearing of 1.00 (SE = 0.064). However, the model is based on only three years of monitoring, and accounts for only about half of the variation in number of years colonies appeared (R² adjusted = 0.48). Variables associated with the sizes and distances of nearest other populations and colonies failed to enter the preliminary model. Bivariate correlations were not significant ($P > 0.05$) between number of years colonies appeared and both size of nearest population and distance to nearest colony; bivariate correlations with distance to nearest population ($r = -0.43$, $P < 0.01$, $n = 35$), size of nearest colony ($r = 0.43$, $P < 0.01$, $n = 35$), and size of population ($r = 0.35$, $P < 0.05$, $n = 35$) were significant, but did not significantly improve the SMR based on colony size and density.

DISCUSSION

Patterns of co-occurrence and covariation of cover values of *C. m.* subsp. *palustris* described in our study strongly suggest that *Triglochin concinna* is restricted to similar habitat, and should be considered as a potential principal host species. However, the distribution of *C. maritimus* probably depends more on habitat preferences than the distribution of a specific host (Chuang and Heckard 1971; Vanderwier and Newman 1984). During the hot, dry summers in southern California, the formation of haustorial connections probably permits *C. m.* ssp. *maritimus* to grow and flower, by providing access to water and/or nutrients late in the season when other annuals have completed their life cycles (Chuang and Heckard 1971; Vanderwier and Newman 1984). Experimental cultivation in pots indicated that *C. m.* spp. *maritimus* is more salt tolerant if grown with a host plant (Fink and Zedler 1989). However, *C. m.* subsp. *palustris* may depend less on the parasitic use of resources than *C. m.* subsp.

maritimus does because of more extended periods of seasonal rainfall and the regular occurrence of summer fog in northern California. Therefore, *C. m.* subsp. *palustris* may be less dependent on the distribution of host species on Tomales Bay than is *C. m.* subsp. *maritimus* in southern California salt marshes.

Limonium californicum was an important predictor of *C. m.* subsp. *palustris* among Tomales Bay marshes, and has been cited by others as an associate of *C. maritimus* (Chuang and Heckard 1971) and *C. m.* subsp. *maritimus* (Vanderwier and Newman 1984; Dunn 1987). At Walker Creek Delta, a positive (although non-significant) bivariate correlation between *L. californicum* and *C. m.* subsp. *palustris* cover contrasted with a negative SMR coefficient for *L. californicum*. The negative regression coefficient may have resulted from multicollinearity with other predictors, as suggested by positive bivariate correlations ($n = 87$) between *L. californicum* and both other variables in the model (*Triglochin concinna*: $r = 0.44$, $P < 0.001$; species richness: $r = 0.51$, $P < 0.001$). Thus, *L. californicum* typically occurred at low densities (percent cover = 14.0 ± 8.7 , $n = 87$) that did not clearly reflect differences in *C. m.* subsp. *palustris* cover within m^2 quadrats, but was a valuable indicator of suitable habitat.

In contrast, *T. concinna* occurred in relatively dense patches (mean percent cover at Walker Creek Delta = 32.3 ± 27.6). At Tijuana Estuary, grasses were important associates of *C. m.* subsp. *maritimus*, possibly because their fine fibrous roots are easier for haustoria to find and penetrate (J. Zedler, personal communication). *Triglochin concinna* typically forms broad lawn-like patches (Howell 1970) and grows from spreading to ascending rhizomes (Thorne 1993), suggesting a greater host species potential with regard to root tissue availability.

The inverse relationship we found between *C. m.* subsp. *palustris* and *Atriplex triangularis* is probably an indication of habitat limitation. *Atriplex triangularis* is a characteristic species of upper marsh edges, occurring in both upper marsh and upland habitats throughout the salt marsh-grassland ecotone (Josselyn 1983; Macdonald 1988). On Tomales Bay, *A. triangularis* often occurred on small sandy delta marshes that retain relatively little tidal water, or on relatively dry sandy soils along the borders of low barrier dunes that form along the outer edges of delta marshes. Fink and Zedler (1988) cautioned against growing *C. m.* subsp. *maritimus* with *Atriplex watsonii* because of low numbers of flowers produced and reduced biomass during experimental cultivation in pots.

Vanderwier and Newman (1984) verified haustorial connections between *C. m.* ssp. *maritimus* and *Distichlis spicata* in the field, and found that *D. spicata* was the only species that was always associated with *C. m.* subsp. *maritimus* at Mugu Lagoon, California. In pot experiments of host associations of *C. m.* subsp. *maritimus*, Fink

and Zedler (1990) found the greatest above-ground biomass when plants were grown with *D. spicata*. *Distichlis spicata* occurred in nearly all of Tomales Bay-wide (94.7%) and Walker Creek Delta (96.6%) observations, regardless of *C. m.* subsp. *palustris* occurrence, and *C. m.* subsp. *palustris* cover at Walker Creek Delta was uncorrelated with *D. spicata*.

The SMR of plant species cover and richness accounted for less than half of the cover variation of *C. m.* subsp. *palustris* at Walker Creek Delta, but corroborated the value of *Triglochin concinna* suggested in the Tomales Bay-wide survey. However, the most important predictor of *C. m.* subsp. *palustris* cover was species richness rather than any particular species. Greater *C. m.* subsp. *palustris* cover in quadrats with greater numbers of species may reflect shared opportunities provided by greater light penetration in areas with lower overall vegetation height not dominated by *Salicornia virginica* (Table 1). Vegetation height was inversely related to species richness ($r = -0.54$, $P < 0.001$, $n = 87$) and directly related to *S. virginica* cover ($r = 0.61$, $P < 0.001$, $n = 87$). Clipping experiments by Fink and Zedler (1989) also suggested that habitat with greater light penetration should support greater seedling densities.

Although Zedler et al. (1992) reported peak growth of *C. m.* subsp. *maritimus* at 20% shade, our data do not suggest greater *C. m.* subsp. *palustris* cover in partially shaded areas. At Walker Creek Delta, vegetation height in quadrats containing *C. m.* subsp. *palustris* was low ($\bar{x} = 12.5 \pm 3.1$ cm), generally including some percentage of bare ground ($\bar{x} = 4.0 \pm 5.4$). We examined bivariate plots and found no evidence that greater *C. m.* subsp. *palustris* cover was related to partial overall cover, as indexed by vegetation height and bare ground. The value of partial shade may therefore be limited to relatively drier summer conditions found in southern California.

Zedler et al. (1992) reported the occasional failure of colonies to germinate, followed by reappearance after a year or two, and suggested the timing and amount of spring rainfall as possible controls. Therefore, a monitoring period much longer than our three-year study, encompassing a greater range of rainfall conditions is probably necessary to describe factors influencing the stability of colonies. The model we have presented provides a preliminary look at the relative importance of size, distance, and distribution among colonies, but should not be used to predict patch stability or minimum patch size.

Our results suggest that the annual probability of a colony appearing is influenced predominantly by colony size and density, and affected little, if at all, by the size or distance of nearby colonies or populations as sources for recolonization or outside recruitment. This is consistent with Dunn's (1987) suggestion that *C. maritimus* distributions are limited by a reduced probability of dispersal to new

locations within a marsh. The apparently low influence of nearby colonies suggests low dispersal probabilities that could limit resiliency to local disturbance. Colony size and density, and therefore the annual probability of a colony to appear, were likely influenced by other underlying factors or processes related to reproduction, growth, and/or survival, including soil salinity, light penetration, and availability of water or nutrients (possibly mediated by the availability of host plants).

Patterns of species co-occurrence and other habitat characteristics described in this paper should aid in predicting suitable habitat areas for *C. m.* subsp. *palustris*. These patterns also suggest that *Triglochin concinna*, and perhaps *Limonium californicum*, may be principal host species. Additional work is needed to understand the degree of isolation among colonies, i.e., to test our speculations that the stability of colonies is limited primarily by colony size and density rather than by the sizes or distances of neighboring colonies or populations, and that dispersal among populations may be insufficient to buffer the potential negative effects of local disturbance.

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